

UNUSUAL GENETIC VARIATION IN BODY SIZE, DEVELOPMENT TIMES, OIL STORAGE, AND SURVIVORSHIP IN THE MARINE COPEPOD *PSEUDOCALANUS*

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The techniques of quantitative genetics have long been applied to animal breeding and agriculture, but seldom to studies of natural populations, and even more seldom to marine organisms. Yet they are the only techniques that can be used to study inheritance of most traits of interest to ecologists and evolutionary biologists. The best introduction remains the book by Falconer (1960).

A previous study of the heritability of demographic traits in the marine copepod *Eurytemora herdmani*, although evidently the first of its kind, produced few surprises (McLaren, 1976a). It was found that traits of such obvious demographic importance as body size (influencing fecundity), age of maturity, and mortality had low heritabilities at laboratory temperatures experienced in nature. As McLaren (1976a) notes, such low heritabilities are expected for traits involved in determining fitness. The results of the present study are very different and not so easy to understand.

In what follows it will be clear that we may be dealing with a genetically complex population of animals, and possibly with cryptic or sibling species. Therefore, we refer throughout only to the genus name, *Pseudocalanus*. The genus is among the most widespread and numerically abundant metazoans in the world (Corkett and McLaren, 1978).

MATERIALS AND METHODS

Three experiments are reported in this study. In the first experiment fertile females were selected for extreme sizes from a sample taken near Halifax, Nova Scotia, in February, 1975. Offspring were kept at 10° C in individual 25 ml vials and fed on a variable schedule with the flagellate *Isochrysis galbana*. No attempt was made to keep track of precise development times, but these were certainly retarded beyond those predicted for conditions of food satiation (McLaren, 1974). Seventeen female and four male offspring reached maturity. The cephalothorax lengths of female offspring were measured for comparison with sizes of their female parents (dams). The resemblance between offspring and dams was analyzed by regression to estimate heritability of size.

The second, more extensive experiment was carried out with parents from a sample taken in mid-May, 1975. Experimental designs, rearing methods, and biometrical techniques were largely the same as those used previously for another copepod by McLaren (1976a) and are outlined briefly here. Seventy-five adult males were placed in bottles, each with about 5 immature females in copepodid stage V (hereafter C-V). Neither males nor females were consciously selected or combined with respect to body size or any other trait. Excess food allowed most

TABLE I

ANOVA and heritability estimates of traits of female offspring of *Pseudocalanus* reared in the laboratory at 10°.

Trait	Source of variance	Mean square	d.f.	Proportion of total variance	P of F**	h ² **
Body size	Between sires	34.61	8	0.230	0.02	0.92
	Between dams, within sires	5.77 (5.48)*	12 (6.6)	-0.021	0.60	0
	Within families	6.80	112	0.790	—	—
Age of maturity	Between sires	77.97	8	0.140	0.13	0.56
	Between dams, within sires	31.63 (35.90)	12 (9.9)	0.148	0.02	0.59
	Within families	14.32	115	0.712	—	—
Time, N-I to C-I	Between sires	21.39	8	-0.110	0.82	0
	Between dams, within sires	34.55 (40.96)	12 (10.8)	0.367	<0.001	1.47
	Within families	8.96	114	0.743	—	—
Time, C-I to adult	Between sires	30.53	8	0.252	<0.001	—
	Between dams, within sires	3.62 (3.06)	12 (5.4)	-0.053	—	—
	Within families	5.89	114	0.801	—	—
Relative size of oil sac	Between sires	13.98	8	0.193	<0.001	—
	Between dams, within sires	2.18 (1.66)	12 (3.9)	-0.064	—	—
	Within families	3.73	115	0.871	—	—

* Terms in parentheses are for reduced d.f., due to unequal class sizes.

** These are based on pooled sums of squares where intermediate level mean squares are non-significant, using the criteria in Sokal and Rohlf (1969); see text.

females to mature, but only a portion of these were successfully fertilized. Females were inseminated only shortly after maturing, and those carrying fertile egg sacs were isolated thereafter. Cephalothorax lengths of parents were measured. The experimental design (see below) called for the rearing of families produced by more than one dam mated to the same male (sire). The families of all such dams (apart from a few whose dams were lost or killed during handling) were reared. A few additional families of single dams mated to individual sires were also reared for regression analyses. The numbers of successful matings and rearings will be summarized in the Results. An attempt was made to obtain a minimum of 18 nauplii (usually two successive clutches) from each dam, but this was not always possible. The experiment was begun with large numbers of stage I nauplii (hereafter N-I) hatched between May 31 and June 7 at times known to within a few hours. Rearing was highly labor-intensive. Each N-I was placed in an individual 25 ml vial, labelled with coded numbers, and placed and treated randomly in a 12L:12D light cycle at 10° C. Food for the offspring consisted of 4-day-old cultures of *I. galbana*, diluted to about 3×10^5 cells per ml with sterilized, enriched sea water to form a culture medium. Every fourth day the animal was removed from its vial by eye-dropper and its culture medium changed. Vials with young animals were checked daily so that time to molting into copepodid stage I (hereafter C-I) was established to within about 0.5 day. The animals were checked more frequently thereafter and age of maturity determined to within a few hours. After maturity, animals were removed from their vials and their cephalothorax lengths measured. An outline drawing of the amount of oil (probably largely wax esters, forming a discrete globule, often called an oil sac) was made on a standardized outline of a cephalothorax length; thus, the relative amount of oil, independent of body size, could be ascertained.

The individuals reared in the laboratory in this experiment were either members

TABLE II

ANOVA for binomial data of survivorship to maturity of *Pseudocalanus*, with estimates of h^2 made after probit transformation (see text).

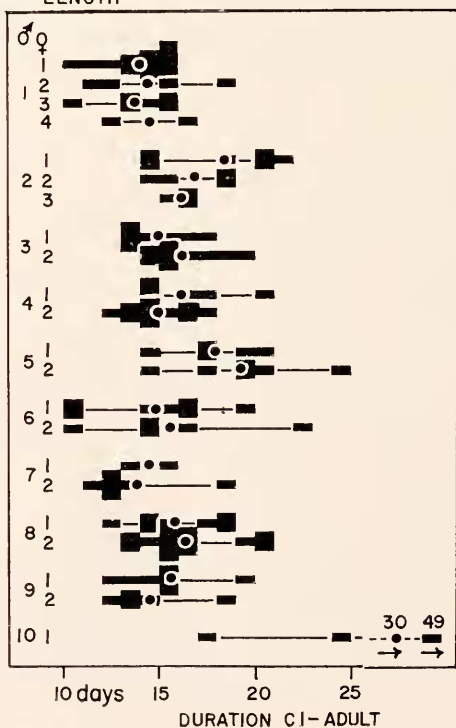
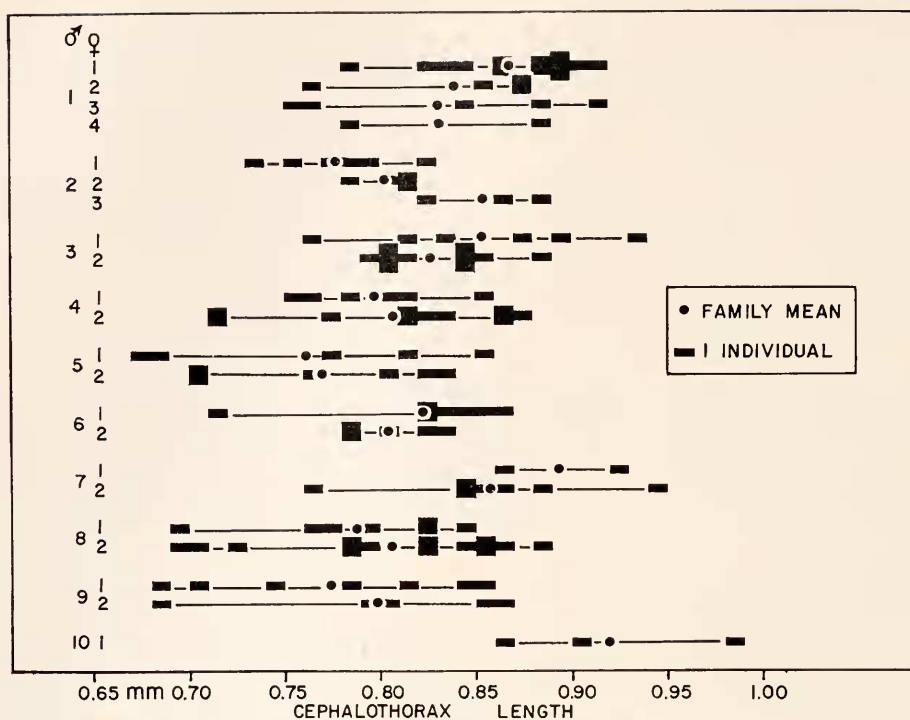
Source of variance	Mean square	d.f.	Proportion of total variance	P of F	h^2
Between sires	0.340	8	-0.022	0.74	-0.08*
Between dams, within sires	0.539	13	0.076	0.005	0.21
Within families	0.227	347	0.946	—	—

* To be taken as zero.

of the same family (full sibs) or members of families with the same sire but different dams (half sibs). The phenotypic values for six traits (Tables I and II) were analyzed by nested ANOVA, which partitions the phenotypic variance into three components: first, between sires; secondly, between dams within sires; and thirdly, within families (among full sibs from individual dams). These *observational components* should be distinguished from the *causal components*, such as additive genetics variance. Tables I and II do not give direct values for the observational components, but rather express them as proportions of the total variance (*i.e.*, intraclass correlation coefficients). In estimating heritabilities (h^2) of traits from such analyses, the intraclass correlation coefficients between dams within sires are normally multiplied by 4. However, on Table I, where intermediate-level mean squares were non-significant, sums of squares have been pooled, and F ratios and proportions of total variances are recalculated using the decision rules outlined by Sokal and Rohlf (1969). Thus the tabulated proportions of total variance do not always agree with tabulated h^2 values. Survivorship in this second experiment (Table II) is a "threshold" trait (*i.e.*, not continuous like the traits on Table I) for which variance components can be estimated by ANOVA for binomial data (Lush, Lamoreux and Hazel, 1948). Heritabilities on the observed probability scale can then be calculated after probit transformation of variance proportions (Dempster and Lerner, 1950, and references therein).

As will be shown in the discussion, there are statistical and genetic reasons for doubting that these values for h^2 in Tables I and II are true intrapopulation estimates. However, the significance of the tabulated F ratios of the underlying mean squares attest to the reality of the various mean differences that will be discussed.

The third experiment was to look at effects of oil storage on the development of late copepodid stages. Samples were taken near Halifax in mid-to-late August, 1976. From these, C-IV (and some C-V of larger animals, which were scarce as C-IV) were placed in 125 ml bottles on a revolving wheel (1 rpm) at 10° C and fed periodically with *I. galbana* and the diatom *Thalassiosira* sp. Animals were chosen to give a wide range of sizes of bodies and oil sacs. Amounts of oil in C-V stages as percentages of body volumes were estimated from sketches, using scaled-up models made of modelling clay and determining displacement volumes. Individuals were observed periodically to estimate times spent in C-V (some did not mature before the termination of the experiment).



RESULTS

Mating and rearing success in the second experiment

Of the 75 males that were offered females, only 23 were successful: 12 mated with 1 dam, 4 with 2, 3 with 3, 1 with 4, and 1 with 5, giving a total of 38 fertilized dams. One successful mating occurred between a very large male (1.02 mm) and a large female (1.09 mm). Other sires whose offspring were reared averaged 0.80 mm (range 0.77–0.84 mm, s.d. 0.022 mm) and their dams averaged 0.97 mm (0.90–1.03 mm, s.d. 0.037 mm). With the inclusion of the large pair, there was evidence of positive size-assortative mating (regression $F_{1,11} = 5.02$, $P \sim 0.05$); without it, there was none ($F_{1,10} = 0.23$, n.s.). In view of the distinct gap in size between the large pair and other parents, subsequent regressions are calculated both with and without the large pair and their offspring (as a single full-sib family, these offspring could not be used in the ANOVA). This family also had some special characteristics that will be referred to later.

Some of the families of the 38 fertilized females were not used because of accidental loss of adults or shortages of young, and others were discarded because they were single full-sib families, unusable in ANOVA. In all, of 441 nauplii of 27 families of 13 sires at the start of the second experiment, 171 belonging to 26 families of the 13 sires were reared to adulthood. Only 14 of these were males, so that (except in survivorship) only female offspring were sufficiently abundant for statistical analyses. Of these, 147 individuals belonged to 21 families produced by 9 sires that had more than one dam. These half-sib and full-sib families could be used in the ANOVA (another family that died out was used in survivorship analysis), and are pictorially summarized on Figure 1 (together with the single full-sib family referred to above). The remaining 5 full-sib families could be used in regression analyses.

Body size

The first experiment used fertile females collected from nature and selected to represent size extremes, and sizes of the 17 female offspring successfully reared (only 4 males were reared, and were discarded) were strongly related to those of their dams (Fig. 2). The weighted regression coefficient (Falconer, 1963) of 0.49 is normally doubled to give an estimate of $h^2 = 0.98$. The selection of parents as such should give negligible bias in estimating h^2 from regression (Hill, 1970). However, in view of the fact that parents were reared in a different (and variable) environment, and because of evidence (below) that parents of such extreme size may not represent interbreeding genotypes, this high estimate of h^2 must be viewed with caution.

In the second experiment, unlike the first, there was no significant regression (at $P < 0.05$) of sizes of female sibs on sizes of their parents. Weighted regressions (as for Fig. 2) of cephalothorax lengths gave the following: $F_{1,11} = 3.60$ for mean offspring on all sires, and $F_{1,10} = 0.04$ when the large sire (10 on Fig. 1)

FIGURE 1. Distribution of three traits among female offspring of 21 families used in the ANOVA of sib traits. Sires and their dams are numbered. Offspring of the single family of sire 10 are also included as an extreme case, discussed in the text.

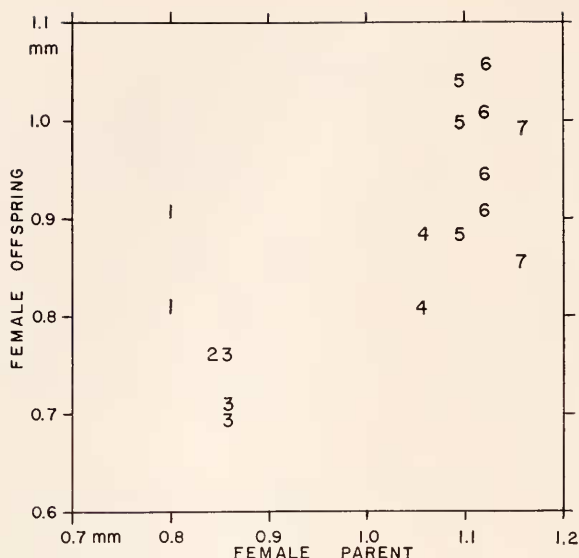


FIGURE 2. Offspring-parent regression. The seven females whose young were successfully reared were chosen from among those of near-extreme size in the sample from nature. Individual offspring are designated by a number indicating the family to which they belong. The weighted regression coefficient (see text) is $b \pm \text{s.e.}_b = 0.49 \pm 0.155$; $F_{1,5} = 7.02$, $P \sim 0.005$.

and his family are excluded; $F_{1,22} = 2.19$ for mean offspring on all dams, and $F_{1,21} = 0.31$ when the dam of the large sire and her family are excluded. It is important to note that the wild-caught parents in this experiment exhibited much narrower size ranges (see above) than did those used in the first experiment (cf. Fig. 2).

Unlike regression analysis, ANOVA of sib traits is designed to estimate heritabilities in a controlled environment independently of phenotypic variance of the parents. The cephalothorax lengths analyzed by the ANOVA are shown on Figure 1, where a strong pattern is evident: half-sib families tend to have very similar mean lengths. The ANOVA (Table I) quantifies this pattern, revealing that the proportion of variance between sires was very high, whereas that between dams within sires was negligible.

Development time

Time taken to reach maturity showed a very different pattern from that for size. The proportions of variance between sires and between dams within sires are about equal, the sire contribution not quite significant by F-test because of lower d.f. (age of maturity, between sires on Table I). However, durations of the period up to appearance of C-I and the period between C-I and maturity appeared to be under very different control. This can be seen on Figure 1, where means for half-sib families differ considerably for duration of N-I to C-I, but show marked similarity for C-I to adulthood. The ANOVA expresses this as a negligible proportion of

variance between sires and a very high proportion between dams within sires during the early part of life, and quite the reverse in the later part of life (Table I). Combined, these two effects lead to roughly equal proportions of variance contributed by dam and sire for the whole developmental period (age of maturity, Table I).

The expected temperature dependent durations in adequate food for the durations from N-I to C-I and from C-I to adult female are about 14 and 16 days respectively (McLaren, 1974; Corkett and McLaren, 1978). As indicated on Figure 1, earlier stages were on average retarded (mean 17.9 days for families used in the ANOVA), but later stages were not (mean 15.6 days).

One offspring of the aforementioned large pair (sire 10 and his mate on Fig. 1) behaved anomalously. It spent 49 days between C-I and adulthood, largely because this offspring was suspended in C-V for some weeks. Its two sibs showed no such pattern.

Survivorship

Overall survivorship in the rearing experiment was 39% and was significantly influenced by differences between dams within sires, but not by sires (Table II). Most animals died in early stages and many spent excessively long times as nauplii before succumbing. Even those that survived tended to be retarded in early, but not later stages (see *Development time* above). Because of the way records were kept, it is not possible to test for differences in survival between early and late

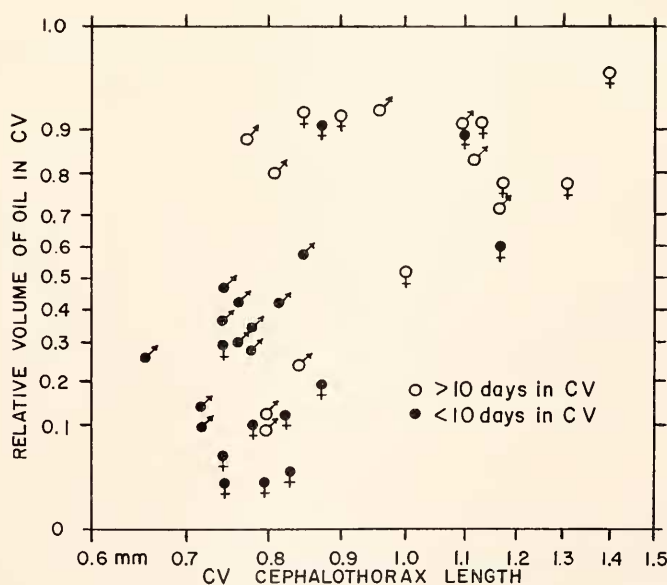


FIGURE 3. Relationships among body size, relative size of oil sac, and suspension of development in a resting stage V copepodid (C V). Relative volume of oil measured as described in the text. Percentage scale transformed by arcsine $\sqrt{\%}$ and cephalothorax length by logarithm, to linearize the relationship.

TABLE III

Spearman rank correlations r_s of body size with development times and relative amounts of oil. Medians of traits in 21 families (with $n > 2$) used in the correlations.

Test	r_s	P
Time N-I to C-I vs. cephalothorax length	-0.21	n.s.
Time C-I to adult vs. cephalothorax length	-0.59	0.01
Relative size of oil sac vs. cephalothorax length	0.65	0.01

stages, but it appears from indirect evidence that most mortality and therefore the strong between-dam, within sire effect, is early in life.

Oil storage

The ANOVA of relative size of the oil sac among offspring in the second experiment showed the same pattern as that for size and for duration of development from C-I to adult. The proportion of variance between sires was very large, whereas that between dams, within sires was negligible (Table I).

The animals secured from samples from nature for the third experiment were chosen for a wide size range, and some small individuals with a large amount of oil (*against* the trend indicated on Fig. 3) were also selected. Thus a formal regression analysis would not be legitimate, but it is obvious (Fig. 3) that larger animals in general had relatively more oil and that most animals that had large amounts of oil also spent long times suspended in C-V.

Again, the large pair (sire 10 and his dam, Fig. 1) produced unusual offspring. Two contained relatively more oil than any other animals reared, and the third had relatively more oil than all but 4 of 158 offspring in which the oil was measured.

Correlations among traits in offspring

Among offspring reared in the second experiment there was marked negative correlation of body size with duration of C-I to adult and positive correlation with size of oil sac (Table III). This analysis excluded the offspring of the large pair (sire 10 and his dam, Fig. 1), which were anomalous in mean duration of C-I to adult (see *Development time*, above). The individual of this family with the largest amount of oil of any of those reared was also the one that entered a prolonged resting stage in C-V, paralleling the trend described for animals from nature (see *Oil storage* above, and Fig. 3).

DISCUSSION

The results pose two main problems for interpretation. First, the regressions of sizes of offspring on sizes of parents used in the second experiment were not significant, whereas the ANOVA revealed strong resemblances in size among offspring of the same half-sib family. Secondly, the ANOVA showed significant between-sire contributions to variance of offspring body size ($P < 0.05$), time between C-I and adult ($P < 0.001$), and size of oil sac ($P < 0.001$), yet the between-dam, within-sire contributions to these same traits were extremely low and non-significant.

(The very large between-dam, within-sire components in duration of N-I to C-I and survivorship is less problematic, and will be considered below).

The first problem is readily explained by the fact that the parents used in the regression analyses were caught in nature, where much of the variation in their size was probably environmentally induced. McLaren (1963, 1965) inferred from seasonal samples that temperature was the main cause of size variation, and Lock and McLaren (1970) showed that animals reared from C-III to adult female at 5° C averaged 10 to 12% longer than those reared at 12° C. This variation is not much exceeded by the difference between the smallest (0.90 mm) and largest (1.02 mm) dam producing offspring for the ANOVA. As already noted, this phenotypic variance of parents did not affect the ANOVA of sib traits. On the other hand, the largest dam producing offspring in the "first" experiment was fully 45% longer than the smallest. Because of this large difference there was some *a priori* expectation of genetic differences among the smallest and largest families. Indeed, the very high h^2 based on such small samples (see Results and Fig. 2) could itself be interpreted as meaning that the extreme dams chosen represented two species, although they did not differ in any obvious way except in size. It was partly because of these preliminary results that no choice of parents was made in the second experiment.

The second problem poses difficulties in terms of the *casual components* of variance among offspring in the ANOVA. The between-sire proportion of variance is an estimate of the additive genetic variance (*i.e.*, h^2 in the strict sense) of the traits on Table I, whereas the between-dam, within-sire proportion includes non-additive genetic variance (*e.g.*, dominance effects), and maternal and common environment effects as well. Thus, normally in such ANOVA of sib traits the between-dam, within sire proportion of variance if anything exceeds the between-sire proportion (*e.g.*, in the copepod *Eurytemora herdmanni*; McLaren, 1976a).

It is very unlikely that the sires could, in fact, have contributed exclusively to the additive genetic variance of such disparate quantitative traits. Although the highly distorted sex ratio (which has occurred in some, but not all experiments with *Pseudocalanus*; see Corkett and McLaren, 1978) is unusual, no obvious mechanism would link it to inheritance through the sire alone.

The only mechanism that appears to account for the results in the ANOVA is assortative mating among parents with respect to *genotype* for body size and correlated traits. In the nested ANOVA design, if sires have mated with dams close to their own genotype for a quantitative trait, then the additive genetic variance contributed by dams will be masked. The rather low mating success, also found by Hart and McLaren (1978) for *Pseudocalanus*, but not by McLaren (1976a) for *Eurytemora herdmanni*, suggests that in general mate choice was problematical. Observations of mating "dances" and probable pheromones in *Pseudocalanus* by Griffiths and Frost (1976) may also signify a certain fastidiousness in mate choice. Hart and McLaren (1978) found size-assortative mating by phenotype over a wider range of cephalothorax lengths (males 0.66–0.98 mm, females 0.85–1.03 mm), but this could only be shown in the present experiment with the inclusion of the unusually large pair (sire 10 and his dam, Fig. 1). Among parents producing young for the ANOVA, size as such could not have been used as a phenotypic mating cue by genetically varied mates.

A simple explanation of our results would be that two or more cryptic or sibling species were involved among potential parents, and that genetic differences in size and correlated traits only became phenotypically manifest among their offspring reared in controlled conditions in the laboratory. There is haphazard evidence for the occurrence of "species" of *Pseudocalanus*, differing in size and showing overlapping geographical ranges (see below). However, *a posteriori* analyses (SNK tests; Sokal and Rohlf, 1969) confirm what seems to be obvious on Figure 1: there is no grouping (at $P < 0.05$) of means of traits of half-sib families into two or more classes that might represent species.

Thus the evidence indicates that the population represented in the ANOVA showed "continuous" variation in genotype for the traits that were measured, and somehow responded to this variation by assortative mating. Although this explains the very high between-sire proportions of variance, it also throws doubt on the actual estimates of h^2 on Table I and II; the statistical and genetical theories underlying such calculations assume random matings of sires and dams.

A possible genetic mechanism underlying size differences in *Pseudocalanus* has already been posed. McLaren, Woods and Shea, (1966) discovered that a large and small form coexisting in a landlocked arctic fiord in Canada had very different DNA content in embryonic nuclei. Woods (1969) concluded that an increase in DNA content of nuclei of this large form probably increased cell size, which in turn would increase body size, if cell number is determinate. Among adult females from Halifax, body size is also strongly correlated with amount of DNA in somatic nuclei (McLaren, 1976b). These curious findings are being explored for publication elsewhere, but clearly may provide a basis for high heritabilities (whether "within" or "among" populations) of body size in the rearing experiment.

Large between-dam, within sire proportions of variance for duration of early stages (N-I to C-I on Table I) and survivorship (Table II) have also been found in traits of the copepod *Eurytemora herdmani* (McLaren, 1976a). Such a pattern is well known in quantitative traits, and the important casual components of such high variance are usually maternal and common-environment effects. It is interesting that in the ANOVA, the observational component of variance was high only in early development and survivorship. Nauplii of *Pseudocalanus* are able to develop up to N-III without food (Corkett and McLaren, 1978). Unhealthy or inadequately nourished dams may have produced young that were less able to develop and survive through critical periods in early life, suggesting a mechanism through which maternal and common-environment effects may operate to produce high between-dam, within sire variance.

The traits examined have demographic significance. Corkett and McLaren (1978) showed that *Pseudocalanus* in temperate waters may undergo several generations of temperature-dependent lengths, uninhibited by evident food shortages. This means that heritable variance in age of maturity and adult female body size (which determines clutch size; McLaren, 1965) could be expressed in nature, as in the laboratory. The negative correlation between body size and development time (Table III) would seem to offer scope for directional selection of shorter generations and larger clutches combined, since both might be advantageous (cf. McLaren, 1974). However, this negative correlation may break down among wider size ranges: Hart and McLaren (1978) showed that embryonic duration of

Pseudocalanus from Halifax was positively correlated with egg size and body size (including a significant partial correlation with size of sire) within the size range over which they demonstrated assortative mating (see above).

Variations in size of oil sac are also probably involved in life-cycle tactics. The oil is clearly an energy store, and is laid down when food is above the level required for maximal rates of growth and reproduction (Corkett and McLaren, 1969, 1978). Most C-V with large amounts of oil among animals collected from nature were clearly in a state of suspended development and most of these were large animals (Fig. 3). These large animals, perhaps also represented by sire 10, his dam and their offspring (Fig. 1), may represent a "species" with a distinct life cycle. In the deeper waters of the Baie-des-Chaleurs, Gulf of St. Lawrence, Lacroix and Filteau (1971) found large C-V animals (mean lengths 1.2–1.3 mm; cf. our Fig. 3) evidently suspended in this stage during summer. They suggested that these were the "form" *major* (= *Pseudocalanus major* G. O. Sars) and that they had an annual life cycle, unlike the smaller "form" which reproduced through the summer.

Probably amount of oil in the smaller animals represented in the ANOVA (Table I) becomes important when they begin to enter overwintering stages. Overwintering stages are known to accumulate as resting C-V before the end of the season of high productivity in some temperate localities (review in Corkett and McLaren, 1978). The present results suggest that larger individuals, whether produced environmentally (temperature; see above) or genetically, would tend to enter a resting stage more readily. These larger individuals would not only be metabolically more secure for a long resting phase than would be the smaller, oil-poor individuals, but would also produce larger clutches upon maturing at the end of winter. A better life-history tactic for genetically smaller individuals might be to forego resting and rather to mature and produce offspring, some of which might be induced by falling temperatures to reach a large size, store more oil, and then enter a resting stage later in the season.

In conclusion, we believe that there is a large amount of genetic variation in *Pseudocalanus* in the waters near Halifax, Nova Scotia. The traits measured are demographically important and possibly subject to strong selective pressures. Although the traits may vary "continuously," at least within certain ranges, the possibility of assortative mating implies that we are not dealing with a single, panmictic population. If, nevertheless, there is enough gene flow among animals represented in our ANOVA so that they might be considered to be a single species, this raises questions about the maintenance of such variation in nature. If the results are interpreted as indicating a complex of species, however difficult to define, then this raises questions about the coexistence of such species in nature. Whatever the true situation, it may also pose problems for conventional systematic analysis and nomenclature.

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SUMMARY

Body size, development times of copepodid stages, and relative amounts of oil were measured among offspring of *Pseudocalanus* reared in excess food at 10° C in the laboratory. ANOVA of these traits among full-sib and half-sib families showed high proportions of variance contributed between sires (*i.e.*, high heritabilities as normally interpreted), but negligible proportions between dams within sires. Although their parents (of a narrow size range) did not mate assortatively by size, as do those of a wider size range, it is concluded that the suppression of the contribution between dams, within sires, was due to assortative mating, using unknown phenotypic clues, by animals whose genetic differences in size, etc., were unmasked among offspring reared in controlled conditions. Although animals of wider size differences may be distinct species, no significant groupings of traits into two or more classes were found among the offspring treated by ANOVA. Development times of early stages, as well as survivorship (most deaths probably in early life), had high proportions of variance contributed between dams, within sires, and a negligible proportion between sires. These results suggest that underlying maternal and common-environment effects were expressed only early in life. Larger copepodid V stages from nature had relatively more oil and spent longer times developmentally suspended in this stage in the laboratory. Larger animals, whether their size is environmentally or genetically determined, may be more prone to enter such resting stages for overwintering, while smaller animals may benefit more from maturation and further generations. If the animals of the narrower size range near Halifax represent a single species, there are problems about maintenance of genetic variation of their demographically significant traits in nature. If they are a complex of cryptic species, then there are questions about their coexistence. Either situation poses problems for conventional systematics and nomenclature.

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